

Artibeus phaeotis. By Robert M. Timm

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Artibeus phaeotis (Miller, 1902)

Pygmy Fruit-eating Bat

Dermanura phaeotis Miller, 1902:405. Type locality Chichén-Itzá, Yucatán, México.

Dermanura rava Miller, 1902:404. Type locality San Javier, northern [Esmeraldas], Ecuador.

Artibeus turpis Andersen, 1906:422. Type locality Teapa, Tabasco, México.

CONTEXT AND CONTENT. Order Chiroptera, Family Phyllostomidae, Subfamily Stenoderminae, Tribe Stenodermini. The genus *Artibeus* contains some 13 extant species. Three subspecies of *A. phaeotis* are recognized (Davis, 1970):

A. p. phaeotis (Miller, 1902:405), see above (*ravus* Miller and *turpis* Andersen are synonyms).

A. p. nanus Andersen, 1906:423. Type locality Tierra Colorado, Sierra Madre del Sur, Guerrero, México.

A. p. palatinus Davis, 1970:400. Type locality 15 km SW Retalhuleu, 240 ft, Retalhuleu, Guatemala.

DIAGNOSIS. Overall size of *A. phaeotis* is small for stenodermines: head and body length (in mm), 51 to 60; length of hindfoot, 8 to 12; ear length, 14 to 18; length of forearm, 35.2 to 41.8; mass, 8.0 to 15.6 g. The color of the fur is uniform dark (Mummy Brown) or pale grayish brown (Cream-Buff); the fur is moderately thick and soft, and extends to base of forearm. Some geographic variation in color exists; bats from the Pacific lowlands of Costa Rica, Nicaragua, and El Salvador [*A. p. palatinus*] are paler and smaller. Miller (1902:404) reported the color of specimens from Ecuador as "light yellowish-brown, intermediate between the cream-buff and clay color of Ridgway, the upper parts, especially the region behind shoulders, washed with broccoli-brown." The eye is ringed with light brown. There are two pairs of conspicuous broad, white facial stripes. The wing membranes are black except for the second interdigital membrane (dactylopatagium minus), which is unpigmented. The uropatagium is moderate in size, pale, and nearly hairless. The basal half of the forearm, both dorsal and ventral, is well furred. The ears are moderately sized for stenodermines and rounded; they are brown in color and usually, but not always, trimmed with a distinct white edge. The noseleaf is comparatively thick and pointed, and is much longer than broad. The tragus is pointed, the outer margin has three larger and several smaller lobes that appear as coarse serrations. The mentum has a row of small warts along the edge, the largest being in the center, the size then decreases outward with a second row of four small papillae immediately behind the first (Goodwin, 1934).

Davis (1970:395) characterized the species as follows: "(1) wide, slightly haired or nearly naked uropatagium with never more than a trace of a fringe on the free edge near midline; (2) short rostrum with abruptly rising frontals producing a 'domed' cranium; (3) cheek teeth never more than 2/2, the first upper molar with a relatively wide talon that comprises about 25 per cent of the total width of the tooth; (4) four distinct whitish facial stripes and (5) the ears usually, but not always, rimmed with yellowish white."

The dental formula is $i\ 2/2, c\ 1/1, p\ 2/2, m\ 2/2$, total 28. The skull is small, typical in general shape for stenodermines, and characterized by a domed cranium (Fig. 1). The molars are relatively smaller than in similar-sized *Artibeus*; however, M1 has a wider talon (Fig. 2) and m3 is absent (Fig. 3).

GENERAL CHARACTERS. The measurements (in mm) of the holotype of *A. phaeotis* (Davis, 1970:397) include: "Greatest length of skull, 19.0; zygomatic breadth, 11.6; mastoid breadth, 10.1; postorbital constriction, 5.0; maxillary toothrow, 6.0; width across molars, 8.4; length of palate (to front of incisors), 8.2; fore-

arm, 38.5; metacarpal III, 38.2; first phalanx, 13.5; second phalanx, 18.0."

Means and ranges (in parentheses) for cranial measurements (in mm) for *A. phaeotis* (Davis, 1970) include: western México (Sinaloa-Guerrero; $n = 135$), greatest length of skull, 18.47 (17.5 to 19.3), zygomatic breadth, 11.39 (10.7 to 12.0), maxillary toothrow, 5.91 (5.6 to 6.4), length of palate, 7.45 (6.6 to 8.1); western México (Oaxaca-Chiapas; $n = 19$), greatest length of skull, 18.81 (18.0 to 19.5), zygomatic breadth, 11.20 (10.5 to 11.7), maxillary toothrow, 5.91 (5.5 to 6.2), length of palate, 8.05 (7.5 to 8.5); southeastern México, Guatemala, and Belize ($n = 84$ to 124), greatest length of skull, 19.42 (18.3 to 20.3), zygomatic breadth, 11.59 (11.0 to 12.3), maxillary toothrow, 6.15 (5.8 to 6.5), length of palate, 8.47 (7.9 to 9.0); Guatemala, El Salvador, and Nicaragua (Pacific side) ($n = 37$), greatest length of skull, 18.75 (18.0 to 19.7), zygomatic breadth, 11.34 (10.7 to 12.1), maxillary toothrow, 6.00 (5.6 to 6.5), length of palate, 8.31 (7.5 to 9.0); Honduras and Nicaragua (Caribbean side) ($n = 67$), greatest length of skull, 19.26 (18.5 to 20.5), zygomatic breadth, 11.49 (10.8 to 12.2), maxillary toothrow, 6.12 (5.8 to 6.4), length of palate, 8.47 (8.0 to 9.0); Costa Rica (Pacific side) ($n = 34$), greatest length of skull, 18.42 (17.7 to 19.2), zygomatic breadth, 11.05 (10.4 to 11.7), maxillary toothrow, 5.84 (5.6 to 6.1), length of palate, 8.09 (7.5 to 8.5); Costa Rica (Caribbean side) ($n = 7$), greatest length of skull, 19.68 (19.3 to 20.1), zygomatic breadth, 11.81 (11.2 to 12.1), maxillary toothrow, 6.34 (6.2 to 6.5), length of palate, 8.81 (8.5 to 9.2).

Additional measurements and discussions of geographic variation were provided by Albuja (1982), Alvarez (1968), Andersen (1906, 1908), Dalquest (1953), Elliot (1904), Goodwin (1934, 1942, 1969), Jones (1966), Jones et al. (1972), Jones and Lawlor (1965), Lukens and Davis (1957), Miller (1902), Ramírez-Pulido et al. (1977), Rick (1968), Swanepoel and Genoways (1979), and Villa-R. (1967).

DISTRIBUTION. The three subspecies are distributed as follows (Fig. 4): *Artibeus phaeotis nanus* is found in western México from the state of Sinaloa south to Oaxaca (Alvarez, 1968; Andersen, 1908; Baker, 1967; Baker and Greer, 1962; Davis, 1958, 1970; Goodwin, 1942; Harris, 1943; Jones, 1966; Jones et al., 1972; Koop and Baker, 1983; Koopman, 1961; López-Forment et al., 1971; Lukens and Davis, 1957; Ramírez-Pulido and López-Forment, 1979; Ramírez-Pulido et al., 1977; Villa-R., 1967; Watkins et al., 1972; Webb and Baker, 1969); *A. p. palatinus* is found along the Pacific coast of Central America from Chiapas south through Guatemala, El Salvador, Nicaragua, and northern Costa Rica (Davis, 1970; Dickerman et al., 1981; Jones, 1966; Wilson, 1983); *A. p. phaeotis* is found in the Caribbean lowlands of Central America from Veracruz south through Belize, Guatemala, Honduras, Nicaragua, Costa Rica, and Panamá, into Colombia, Venezuela, and extreme northern Brazil, Ecuador, Guyana, and Perú (Albuja, 1982; Allen, 1916a, 1916b; August and Baker, 1982; Baker et al., 1971; Birney et al., 1974; Dalquest, 1953; Davis, 1970; Davis et al., 1964; Dorst, 1951; Eisenberg et al., 1979; Gaumer, 1917; Goodwin, 1934, 1969; Hall and Dalquest, 1963; Harris, 1943; Hershkovitz, 1951; Jones, 1966; Jones and Lawlor, 1965; Jones et al., 1973; Koopman, 1982; Lackey, 1970; McCarthy, 1982; Medellín, 1983; Miller, 1902; Murie, 1935; Rick, 1968; Schalldach, 1964; Sturm et al., 1970; Van Tyne, 1933; Villa-R., 1967).

Pygmy fruit-eating bats have been found at elevations ranging from sea level to 1,200 m, although they seem to be more common at lower altitudes. There is no fossil record for the species.

FORM AND FUNCTION. The anatomy of the brain was described for numerous species of phyllostomids by McDaniel (1976: 168), who reported that the "brain of *Artibeus phaeotis* differs

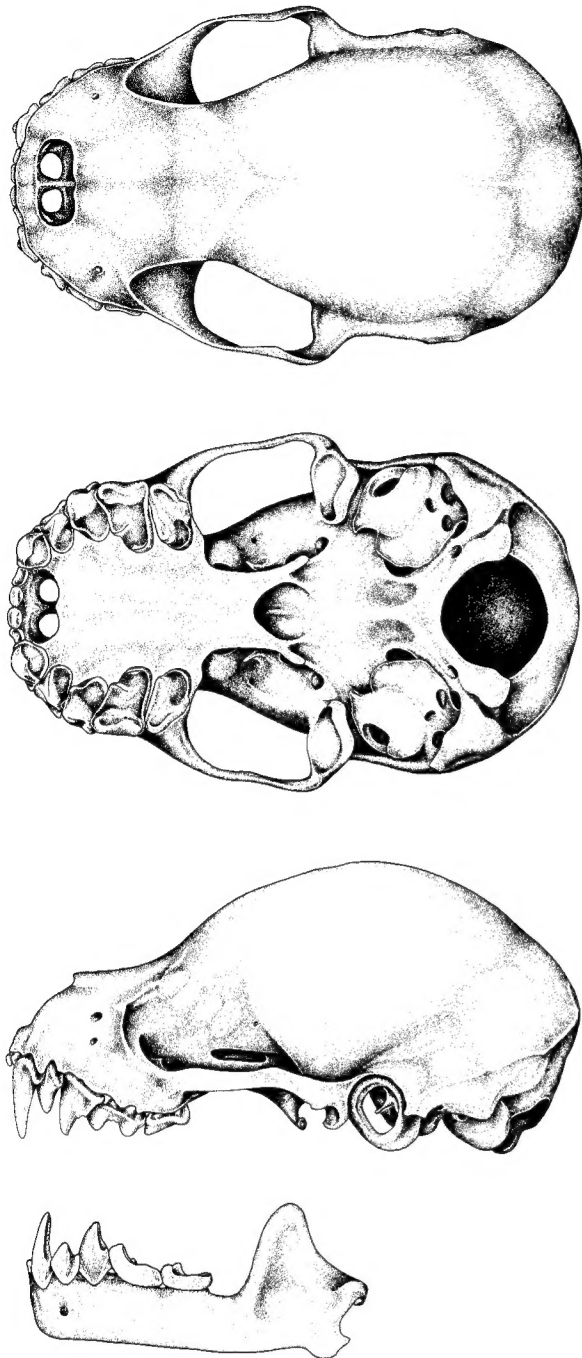


FIG. 1. Dorsal, ventral, and lateral views of the cranium and lateral view of the mandible of an adult female *Artibeus phaeotis palatinus* from 2 km S, 12 km E Bolson, Guanacaste Province, Costa Rica. Greatest length of skull is 17.3 mm.

from those of other species of *Artibeus* in having short and deep cerebral hemispheres, a somewhat domed profile, and dorsally exposed inferior colliculi." Additionally, McDaniel (1976:163) stated "In *Artibeus phaeotis*, the interhemispheric sulcus forms a distinct cingulate sulcus and a smaller callosal sulcus above the corpus callosum. The callosal sulcus is less well developed than in *Artibeus jamaicensis*. Cortical cells overlying the corpus callosum and substantia alba form a slightly denser zone than is formed by other layers of the cortex. The lateral olfactory tracts are ventrally located. The lateral thalamic nuclei project dorsally almost to the level of the habenular nuclei. The thalamus is narrow and deep. The pons is deep and ventrally flattened." Dorsal, ventral, and lateral views of the brain were illustrated by McDaniel (1976).

Forman (1973:916) characterized the stenodermines as hav-



FIG. 2. Ventral view of the left upper tooththrow of *Artibeus phaeotis phaeotis* (FMNH 58580) from El Petén, Tikal National Park, Guatemala.

ing "some development of a cardiac vestibule between the gastroesophageal junction and lesser curvature, a narrow zone of cardiac glands, arrangement of circular muscle fibers into large bundles . . . progressive thickening of the circular muscle layer from the onset of the terminal portion to the pyloric sphincter, a poorly-developed muscularis mucosae . . . and uniformity in the depth of the fundic mucosa." *Artibeus phaeotis* was unique in lacking Brunner's glands on the distal surface of the sphincter. Forman et al. (1979:212) concluded that all seven species of *Artibeus* they examined (*aztecus*, *inopinatus*, *jamaicensis*, *lituratus*, *phaeotis*, *toltecus*, and *watsoni*) "have tremendously enlarged cardiac vestibules that permit temporary storage of large amounts of plant material."

Frugivorous stenodermines possess kidneys composed of only two parts, the cortex and a simple renal medulla (Studier et al., 1983). Insectivorous, carnivorous, and sanguinivorous phyllostomids have a cortex and a complex medulla that is subdivided into an inner and outer zone. *A. phaeotis* has a thin medulla as expressed by the ratio of total medullary thickness (M) to the thickness of the cortex (C) of 2.2. Studier et al. (1983) suggested that the renal index ratio reflected food habits in bats and was not correlated with mesic or xeric habitats or body size. Studier and Wilson (1983) found osmotic pressures of urine in frugivorous phyllostomids to be less than those in other phyllostomids, which were in turn less than in insectivorous bats. Urinary potassium (K^+) levels were highest in frugivorous bats, whereas urinary sodium (Na^+) concentrations showed no differences between frugivorous and non-frugivorous bats (Studier and Wilson, 1983). These same authors concluded that natural urine concentrations were related primarily to diet and secondarily to environmental dehydration pressure.

Phillips et al. (1977) found the ultrastructure of the submandibular salivary gland to be unique among the few species of mammals studied to date. They regarded the submandibular serous secretory cells as typical; however, the seromucoid demilunar mucous



FIG. 3. Dorsal view of the lower jaw of *Artibeus phaeotis* (FMNH 58580).

cells were unique in structure and origin, although the secretory product produced was morphologically similar to that in other mammals (Phillips et al., 1977).

Vaughan (1970) described the dactylopatagium minus along the leading edge of the wing as broad and semi-transparent, with digits two and three permanently spread open. Lack of pigment in the dactylopatagium occurs in several other species of *Artibeus* and in *Centurio senex*, *Chiroderma salvini*, and *Sturnira lilium*, and stands in sharp contrast to the heavily pigmented remainder of the wing (Vaughan, 1970). Vaughan (1970) suggested that the enlarged and permanently spread dactylopatagium was an adaptation to in-

crease camber in the slow flying bats, resulting in increased lift, and that the transparent dactylopatagium was used as a window through which the roosting bats could see the approach of potential predators. Lawlor (1973) found that *A. phaeotis* was typical of the smaller frugivores in having a small wing-aspect ratio. Large bats were found to have smaller wings relative to body size than do small bats, suggesting that small bats may be better able to manipulate proportionally larger wings for their size (Lawlor, 1973). Vaughan and Bateman (1970) found that phyllostomids had generalized wings that were less well adapted for efficient flight than the wings of molossids or vespertilionids; however, the phyllostomid wing allowed for food handling and clambering in vegetation as well as for flight. Smith and Starrett (1979) concluded that the length of the head and body of bats had little effect upon the shape of the wings; generally bats tend to possess wings ranging from 1.5 to 2.5 times the head and body length. They also noted that small-sized bats tended to have longer wings with lighter loading than large bats.

Birney et al. (1976) reported that *A. phaeotis* did not possess the enzyme *L*-gulonolactone oxidase, the catalyst necessary for the synthesis of vitamin C. Thus, like all bats, *A. phaeotis* must obtain vitamin C from the diet.

REPRODUCTION. The reproductive pattern is perhaps best characterized as seasonally polyestrous and bimodal (Bonaccorso, 1979; Fleming et al., 1972; LaVal and Fitch, 1977; Wilson, 1979). Females bear only a single young, as in most phyllostomids. In Costa Rica, *A. phaeotis* has sharply bimodal peaks of reproduction, with 100% of adult females pregnant in April and again in August and September (LaVal and Fitch, 1977). In México, Jones et al. (1972:15) reported capturing four pregnant females at La Cruz, Sinaloa, on 6 July 1962 with "embryos 21–28 mm in crown-rump length." On the Yucatan Peninsula, pregnant females were captured in January, February, March, and August (Jones et al., 1973); on Isla Cozumel, Jones and Lawlor (1965) reported that two females captured in August each carried single embryos, 23 and 25 mm in crown-rump length. In Jalisco, Watkins et al. (1972:21) reported "gravid females . . . for the months of January (six), April (one), and June (11), and a lactating individual was taken in August." Murie (1935:19) reported that a female taken on April 15 [in Guatemala] contained a 30-mm embryo; Jones (1966:459) found a female (March 10) at Toocog, Guatemala, that carried a single, near-term embryo on the left side that measured 26 mm; whereas Rick (1968:519) captured a pregnant female on 6 May at Tikal that contained an embryo 17 mm long, and two on 25 May that contained embryos measuring 7 and 13 mm long. A single pregnant female from Venezuela carrying an embryo 15 mm in crown-rump length in April was reported by August and Baker (1982). An adult female carrying her juvenile male offspring was captured in early May in Quintana Roo (Birney et al., 1974).

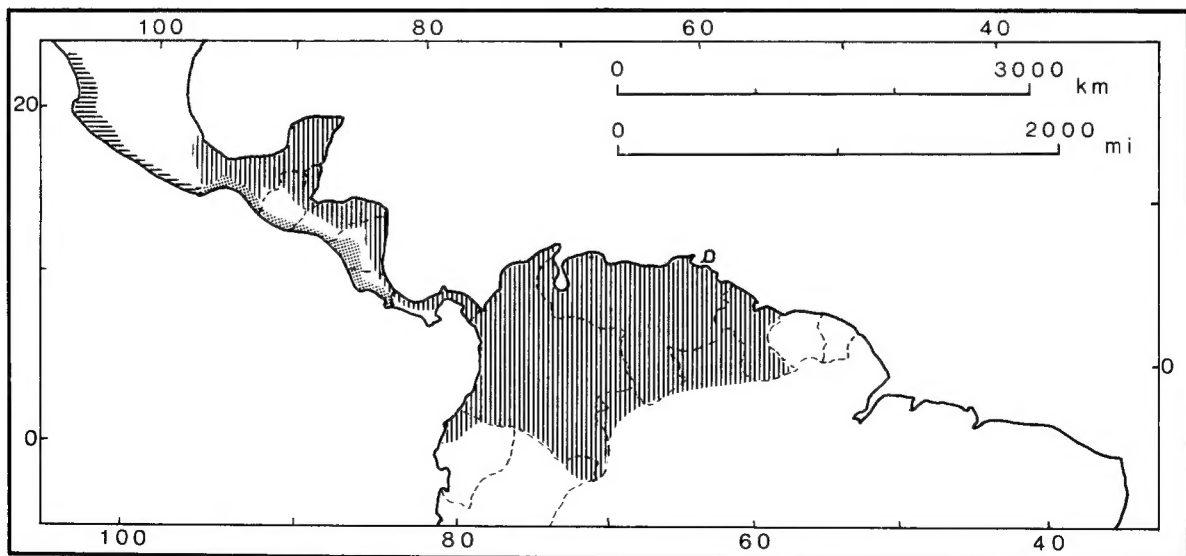


FIG. 4. Map of Central and northern South America showing the distribution of subspecies of *Artibeus phaeotis*. The vertical lines represent *A. p. phaeotis*, the horizontal lines *A. p. nanus*, and the stipple *A. p. palatinus*.



FIG. 5. Photograph of a single adult female *Artibeus phaeotis* roosting in a tent on banana. Details of the cut side veins may be seen along the midrib of the leaf. Photograph by R. M. Timm.

The reproductive cycle of males as reflected by testes measurements seems to vary seasonally, although limited data exist. Ramírez-Pulido et al. (1977) reported that the testes length of 26 males from Guerrero ranged from 4.0 to 8.0 ($\bar{X} = 4.9$). In Sinaloa, Jones et al. (1972:15) reported a male with testes 3 mm long was taken in July, and two collected in October had testes 5.5 and 6 mm long. On the Yucatan Peninsula, Jones et al. (1973) reported that testes measurements for 16 males captured in December, January, and February averaged 4.7 (range 3 to 6). In Jalisco, Watkins et al. (1972) found a November-caught male with testes of 4.5 mm. In Guatemala, Jones (1966) reported that two males captured on 10 March had testes that measured 6 mm, and Rick (1968) reported capturing a male on 11 March with testes that measured 5 mm. Mares and Wilson (1971) reported finding a single male in breeding condition in Costa Rica during the dry season.

ECOLOGY. *Artibeus phaeotis* is primarily frugivorous, although it feeds on pollen and insects to a lesser extent. In Costa Rica, pygmy fruit-eating bats fed on the fruits and pollen of 11 species of plants (Fleming, 1973; Heithaus et al., 1975). *Artibeus phaeotis* seems to be associated primarily with tropical deciduous forest, tropical evergreen forest, dry tropical forest, and thorn forest vegetational communities. Accounts of habitat for pygmy fruit-eating bats (Ramírez-Pulido et al., 1977; Watkins et al., 1972) include mention of their being netted in close proximity to stands of bananas, *Musa sapientum* (Musaceae). Davis (1970) suggested that they roosted under leaves of bananas. In Costa Rica, I found that *A. phaeotis* altered the shape of banana leaves to produce a diurnal roosting structure termed a "tent" by incompletely severing the side veins and interconnecting tissue that extend at right angles from the midrib (Fig. 5). The cuts extended from the base of the leaf to near the tip.

Villa-R. (1967) found a single specimen roosting near the mouth of a small cave. Goodwin (1934) mistakenly reported a bat identified as *A. phaeotis* from a building in Guatemala; the bat was *A. toltecus*.

Parasites known from *Artibeus phaeotis* include mites, *Tecmatlana sandovali* Hoffmann (Trombiculidae), *Periglischus iheringi* Oudemans (Spinturnicidae), *Eudusabekia artibeii* Lukoschus, Scheperboer, Méndez, and Fain and *Eudusabekia viguerasi* (Dusbábek) (Myobiidae), and a batfly of the family Streblidae, *Neotrichobius stenopterus* Wenzel and Aitken (Lukoschus et al., 1981; Timm, pers. observ.; Webb and Loomis, 1977). R. Wenzel (pers. comm.) suggested that *N. stenopterus* is a host-specific parasite of *A. phaeotis*. The only species of endoparasite known from *A. phaeotis* is the nematode *Cheiropteranema globocephala* Sandground, found in the stomach on several occasions (Ubelaker et al., 1977). The trypanosome *Leishmania mexicana* (Biagi) Garnham, the causative agent of leishmaniasis, was reported in *A. phaeotis* from Belize (Disney, 1968). Parasites erroneously reported by Disney (1968) from *Artibeus phaeotis* include the following streblids: *Euctenodes mirabilis* [= *Strebla mirabilis*], *Trichobius dugesii* [misidentification], and *Pterellipsis aranea* [= *Megistopoda aranea*; true host *Artibeus jamaicensis*]. The virus causing Venezuelan

encephalitis was isolated from *A. phaeotis* in Veracruz (Wong-Chia and Scherer, 1971).

Bonaccorso et al. (1976) described an improved technique for marking Neotropical bats, including *A. phaeotis*, with color-coded and numbered aluminum or plastic bird bands. They were able to reduce the frequency and severity of band injuries to the wing by first cutting a small slit in the antebrachial membrane parallel to the radius and passing one end of the band through the slit before clamping it over the radius.

GENETICS. *Artibeus phaeotis* has a diploid number of 30 chromosomes and a fundamental number of 56. The autosomes include 10 pairs of submetacentric and metacentric elements and 4 pairs of subtelocentrics; the X is a subtelocentric (Baker et al., 1982; Hsu et al., 1968). Baker (1967) reported that the autosomal complement and X-chromosome of *A. phaeotis* were indistinguishable from those of *A. jamaicensis*, *A. lituratus*, and *A. toltecus*. Of the Y-chromosome, Baker (1967:419) stated that "only one Y occurs. This Y, however, is biarmed, unlike either of the two Ys of the other three species. It may have been formed by a centric fusion of the two Y elements . . . or if evolution has proceeded in the other direction, the two Y elements have been derived from a centric fission of a Y element similar to that found in *A. [phaeotis]*." Hsu et al. (1968:34) stated that *A. phaeotis* had the "classic XX/XY sex determination system . . . [the] . . . Y chromosome is a small submetacentric." Additionally, they suggested that *A. phaeotis* was more advanced than its sister species because of a Robertsonian fusion between Y₁ and Y₂. The total number of *A. phaeotis* karyotypes reported in the literature to date is four, three males and one female. Karyograms have been illustrated by Baker (1979) and Hsu et al. (1968).

Koop and Baker (1983) suggested that *A. cinereus*, *A. phaeotis*, *A. toltecus*, and *A. watsoni* were derived from a common ancestor and represent relatively recent speciation, because the electrophoretic data indicated few allozymes with fixed differences between the species. Immunological comparisons revealed that *A. phaeotis* has higher immunological affinity with other genera of phyllostomids than it does with the congeneric *A. jamaicensis* (Gerber and Leone, 1971; Valdivieso and Tamsitt, 1974).

REMARKS. The systematic relationships of the smaller *Artibeus* have been problematic for some time and to a certain extent remain so today; *nanus*, *rava*, and *turpis* all were originally described as distinct species. Presence or absence of the third lower molar, size, color, and shape of the cranium have been difficult to evaluate. Hershkovitz (1949) found that the size and presence of a rudimentary tooth (m3) varied both geographically and within local populations, and concluded that it was of little value as a diagnostic character. He presented a provisional classification of the small *Artibeus* that included *phaeotis* as a subspecies of *Artibeus cinereus* and *ravus* as a junior synonym of *A. cinereus*. Several subsequent authors have followed this classification including the listing of *turpis* as a distinct species (Dalquest, 1953; Davis, 1958; Hall and Kelson, 1959; Handley, 1966). However, Jones and Lawlor (1965) concluded that *cinereus* and *phaeotis* are distinct and that *turpis* is synonymous with *phaeotis*. Regarding the minute, peglike m3, Davis (1969) found that it was only present in what he described as the *A. cinereus-glaucus-rosenbergi-watsoni* group, and that taken into account with the width of M1, it was useful in species determinations. Carter and Dolan (1978:63) examined the holotypes of *Artibeus turpis* and *A. nanus* in the British Museum (Natural History) and stated they found "no differences to distinguish the skulls of holotypes for *A. turpis* and *A. nanus*."

The holotype of *A. phaeotis*, an adult female, was collected by E. W. Nelson and E. A. Goldman, and is represented by a skin and skull, National Museum of Natural History (USNM) 108176; it was collected on 10 February 1901; the original number is 14537. I follow Koopman (1982) in treating *A. phaeotis* and *A. ravus* as conspecific. Davis' (1970) revision of *A. phaeotis* considered only the Central American forms; thus, he did not treat the western Ecuador population described as *A. ravus*. Although the name *ravus* has page priority over *phaeotis* in Miller's (1902) original description of the species, I consider *phaeotis* the name of preference because it is the most widely used name in the literature, and its continued use will promote nomenclatorial stability. *A. ravus* had long been considered a subspecies of *A. toltecus* (Jones and Carter, 1976; Allen, 1916a, 1916b).

The specific name *phaeotis* is of Greek derivation coming from the word *phaios*, meaning dusky, and referring to the dusky, grey coloration of this species.

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